JANEIA SILURICA, A LINK BETWEEN NUCULOIDS AND SOLEMYOIDS (BIVALVIA)

by LOUIS LILJEDAHL

ABSTRACT. *Janeia silurica* Liljedahl, 1984 from the Silurian of Gotland has unusual characters in common with the deposit-feeding nuculoids and the systematically controversial solemyoids, generally considered to have a life habit intermediate between deposit- and suspension-feeding but which in fact lives in symbiosis with chemoautotrophic bacteria. The extensive silicified material available is occasionally extremely well-preserved, reflecting soft-part anatomy of the muscles of the foot as well as of the mantle. *J. silurica*, which has conspicuous traces of the pallial muscles of the mantle (fused margins?), probably had an efficient system of cleaning the mantle cavity, a typically solemyoid feature. However, it was probably a more active burrower than the extant *Solemya* since it presumably had a larger foot and smaller gills. The gills were thus used for respiration only, as in nuculoids, while the inferred character of the mantle indicates an evolutionary trend towards the solemyoid life habit.

IN the animal kingdom the suspension-feeding lamellibranch bivalves are regarded as being the most successful exploiters of the almost inexhaustible primary biomass of the oceans, i.e. the plankton supply. The strikingly expanded ctenidia of these bivalves, which are used exclusively for food collecting, occupy most of the mantle cavity and the individual filaments are far more numerous than the protobranch ctenidia of deposit-feeders (nuculoids). Each filament is considerably longer than the short protobranch filament and is thus by far more efficient. In contrast to the lamellibranch ctenidia the protobranch ctenidia are used mainly for respiration.

The affinities of *Solemya* have always been controversial. Gross soft-part morphology points to a relationship with the nuculoids (e.g. Yonge 1941, 1959) but specialization along different lines makes its systematic position uncertain (e.g. Purchon 1978). The life habit of *Solemya* is poorly understood, considered by some to be intermediate between the deposit- and suspension-feeding mode of life (e.g. Yonge 1941) and by others as a suspension-feeder (e.g. Stanley 1970). However, recent discovery of procaryotic symbionts in *S. velum* (Cavanaugh *et al.* 1981) in combination with the fact that the gut of solemyoids is extraordinarily minute, and in some species even completely absent (Reid and Bernard 1980), suggests that these bivalves obtain nutrient mainly through symbiosis with chemoautotrophic bacteria.

Morphological comparison of Janeia silurica *with nuculoids and solenyoids*

The silicified Wenlock fauna at the locality Möllbos 1, Gotland, Sweden contains eleven bivalve species, one of which is *J. silurica* Liljedahl, 1984 (see Liljedahl 1983, 1984 (in press)). This species is represented by more than 500 valves containing extraordinarily well-preserved specimens, some of which exhibit traces of the soft parts.

The discovery of *J. silurica* extended the known stratigraphical range of the solemyoids to the late Early Silurian, the oldest previously known representative being of mid Devonian age (Newell 1969). Pojeta (1978, p. 231, fig. 4) considered an Ordovician nuculoid as showing solemyoid characters (described by Eichwald 1880, p. 991, pl. 39, fig. 10, as *Nucula aedilis*) with the expanded anterior part of the shell and the enlarged anterior adductor muscle scar being the most typical features. I agree that the lateral outline of this species is possibly reminiscent of the solemyoid form (but see also the close similarity in shape with the nuculoid? *Dystactella subnasuta* Hall and Whitfield; see McAlester 1968, p. 27, pl. 5). However, since dentition and other internal features are unknown, it is necessary to await the discovery of better-preserved material to understand its systematic position. Pojeta's (1978)

second example of a nuculoid showing solemyoid features is *Ctenodonta nasuta* (Hall). It is elongate, has a slightly expanded anterior part but a posterior end which is longer than the anterior one (see Salter 1859, pl. 8, fig. 2 and Pojeta 1971, pl. 4, fig. 10).

J. silurica shows certain similarities to the solemyoids combined with a number of primitive features characteristic of extant Nuculoida. The shell of *J. silurica* is thin, as in the extant *Solemya*, and elongate with an extended anterior part (text-fig. 1:1, 2, 3). It is not, however, as strictly cylindrical as that of the extant *Solemya*. The shell of *Solemya* gapes at both ends while in *J. silurica* the valve margins fit together except for the dorsal margin, the left valve overlapping the right (text-fig. 1:5 and 3). Like the extant *Solemya*, the ligament of *J. silurica* consists of a posterior internal/external part and an anterior external part (text-fig. 1:1, 4, 6). The ligament construction was probably strong to judge by the unusually large ligament area (text-fig. 2B).
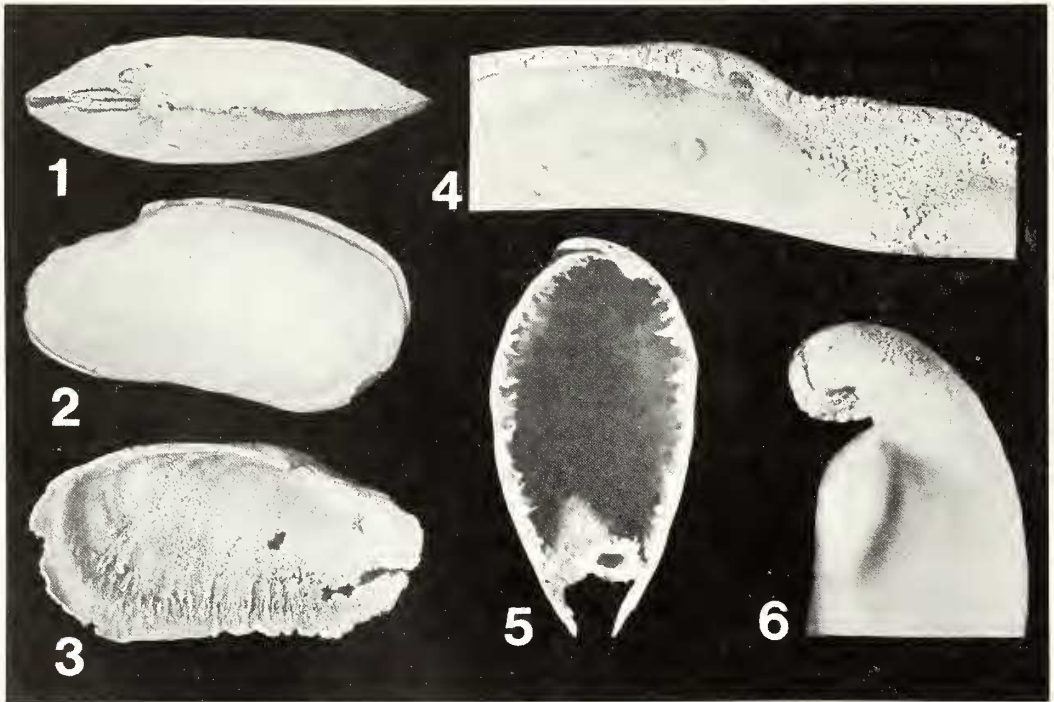

TEXT-FIG. 1. *Janeia silurica* Liljedahl, 1984.

1, External dorsal view of articulated specimen, anterior to the right. SGU 3426/3427, × 1.8, sample G77–29LJ.

2, External lateral view of articulated specimen, anterior to the right. Note overlapping left valve, same specimen as in 1, × 1.8.

3, Internal lateral view of a right valve (holotype). Note conspicuous traces of pallial muscles. SGU 3608, × 2.4, sample G79–79LJ.

4, Internal lateral view of umbonal part of a right valve. Note chondrophore extending above beak. SGU 3318, × 6.1, sample G77–28LJ.

5, Vertical section of an articulated specimen. Note silicified possible folded in ventral margin of the mantle, SGU 3592/3593, × 4.4, sample G79–78LJ.

6, Posterior view of beak and chondrophore, same specimen as 4, × 7.8.

All specimens are in the Type Collection of the Geological Survey of Sweden. The material was coated with ammonium chloride prior to photography.
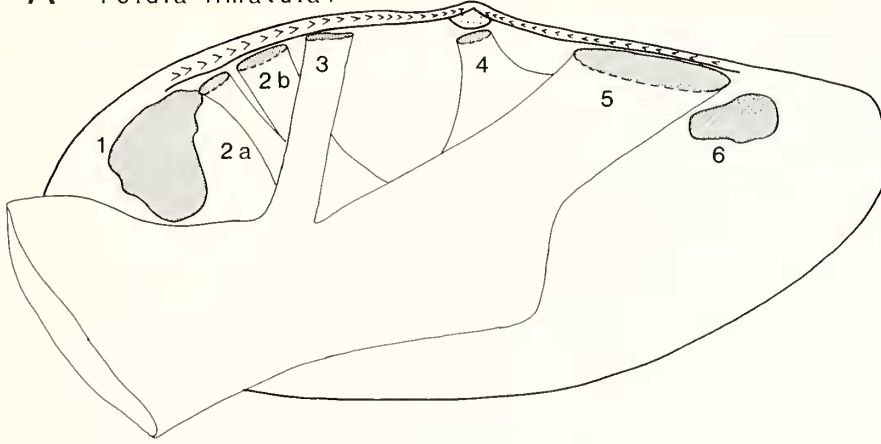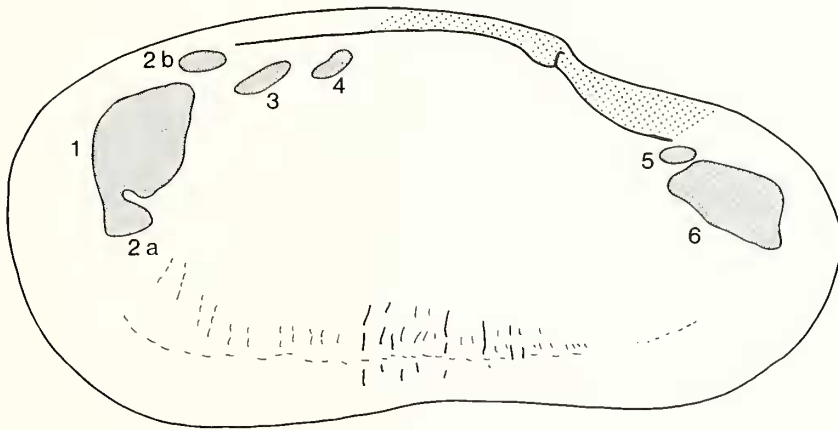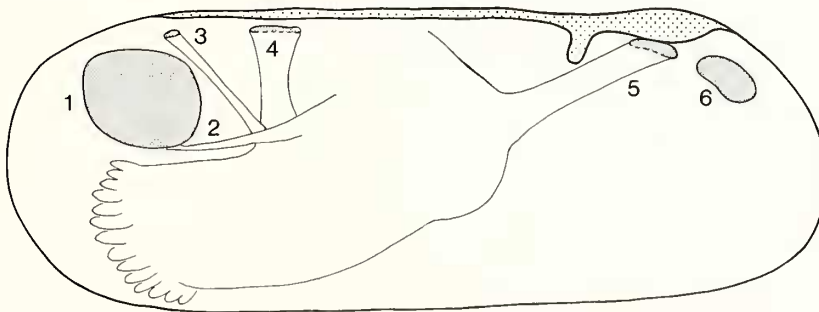
TEXT-FIG. 2. Muscular impressions (densely stippled) and ligament area (loosely stippled). A, *Yoldia limatula*?: 1 = anterior adductor muscle. *2a, 2b* = anterior pedal protractor muscles. 3 = anterior pedal retractor muscle. 4 = pedal elevator muscle (dorsomedian muscle). 5 = posterior pedal retractor muscle. 6 = posterior adductor muscle; note conspicuously large posterior pedal retractor muscle (No. 5). After Heath 1937, pl. 10, fig. 83. B, *Janeia silurica* Liljedahl: 1 = anterior adductor muscle scar. *2a, 2b* = anterior pedal protractor muscle scars. 3 = anterior pedal retractor muscle scar. 4 = pedal elevator muscle scar. 5 = posterior pedal retractor muscle scar. 6 = posterior adductor muscle scar. C, *Solemya togata* Poli: 1 = anterior adductor muscle. 2 = anterior pedal protractor muscle. 3 = anterior pedal retractor muscle. 4 = pedal elevator muscle. 5 = posterior pedal retractor muscle. 6 = posterior adductor muscle. After Pelseneer 1891, pl. 9, fig. 15, ligament extension after Owen 1959, p. 217, fig. 3C.

The muscular impressions of *J. silurica* (text-fig. 2B; see also Liljedahl 1984, fig. 15) are deeply incised, their distribution much resembling that of extant nuculoids (text-fig. 2A; cf. Heath 1937), similarities with *Solemya* also being evident (text-fig. 2C; cf. Pelseneer 1891). The adductor muscle scars are almost equal in size (cf. reduced posterior adductor muscle in extant *Solemya* in Newell 1969, p. N242). The anterior pedal protractors are absent or minute in *Solemya* (2 in text-fig. 2C) but well developed in *J. silurica* (2*a* in text-fig. 2B). Scar 2*b* of *J. silurica* possibly also indicates a pedal protractor muscle since it has a position similar to the most anterior pedal muscles in nuculoids which function as pedal protractors (2*a*, 2*b* in text-fig. 2A). Scar 3 in text-fig. 2B of *J. silurica* may be homologous with the anterior pedal retractor in nuculoids (3 in text-fig. 2A) while scar 4 in text-fig. 2B of *J. silurica* probably corresponds to the pedal elevator in both nuculoids and solemyoids (4 in text-fig. 2A, C). The posterior pedal retractor muscle scar of *J. silurica* (5 in text-fig. 2B) is minute as in solemyoids (5 in text-fig. 2C) in contrast to the extremely large posterior pedal retractor muscle of the nuculoids (5 in text-fig. 2A).

Thus the pattern of pedal muscle scars and the greatly extended anterior part of the shell of *J. silurica* together suggest that the foot was correspondingly enlarged occupying more than half the mantle cavity, and that it protruded from the anteroventral part of the shell. Accordingly it must have had a function similar to that in *Solemya* (cf. Drew 1900; see also Liljedahl 1984, fig. 15 showing a reconstruction of the foot of *J. silurica*).

The conspicuously deep and broad traces of the pallial muscles of *J. silurica*, which are less accentuated in the posterior and anterior extremities, indicate that the radial muscles of the mantle edge were unusually strong (text-fig. 1:3). Because of their uneven impression these scars also suggest partially fused mantle edges (cf. *Solemya* in Drew 1900, p. 264, figs. 9, 10, 11, 12) with one anterior and one posterior opening. If these assumptions are true, then this species was probably able to withdraw the ventral margins of the mantle with great force, perhaps as in *Solemya* (see silicified possible replica of an infolded ventral margin of the mantle in text-fig. 1:5; cf. Drew 1900, pp. 264, 265).

The anteriorly extended shell and the distribution and size of the impressions of the pedal muscles of *J. silurica* indicate that the foot occupied more than half the mantle cavity, thus leaving about a third of the cavity for the ctenidia (cf. ctenidia of solemyoids occupying about half the mantle cavity in Yonge 1941, p. 93). If this assumption holds, then the ctenidia of *J. silurica* were probably not involved in ingestion (as they are to some extent in *Solemya*; Yonge 1941, p. 116) but were used for respiration only, as in nuculaceans (Yonge 1941, pp. 115, 143).

The shape of the shell with its posterior umbonal slope and with the position of the posterior adductor muscle scar, make a strictly posterior exhalant current, as in *Solemya*, improbable in *J. silurica*, the direction presumably being ventroposterior. Thus, unlike *Solemya* it probably did not have free-swimming ability (cf. Drew 1900).

Ecology of extant nuculoids and solemyoids

Extant nuculoids live in soft muddy to sandy bottoms, moving about only sparingly (Yonge 1941, pp. 81, 82). They collect food by means of the extended labial palps, or proboscides, which when
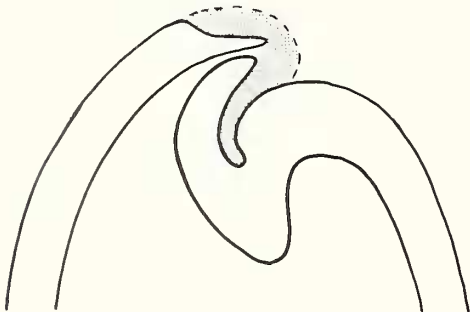
TEXT-FIG. 3. Vertical section of umbonal region of *Janeia silurica* showing chondrophore of right valve and reconstructed ligament (stippled).

protruded between the opened valves collect and guide food particles from the sediment to the mouth (Yonge 1941, p. 114). The protobranch ctenidia, the main function of which is respiration, are fairly small, and though they may possibly be involved in feeding they cannot be compared with those of the lamellibranch bivalves in this respect (Yonge 1941, p. 115).

Extant *Solemya* thrives in rather firm, sandy mud in which it digs itself down in a Y-shaped burrow (Stanley 1970) where it usually stays for the greater part of its time (Yonge 1941, p. 96). The protobranch ctenidium of this genus has a surface comparable with that of a lamellibranch ctenidium and the labial palps are small, not reaching beyond the mantle margins, i.e. they are not able to collect food outside the shell (Yonge 1959, p. 213). *Solemya* inhales water anteriorly by the actions of muscles. The water is heavily laden with suspended sediment, and food particles are transferred by the labial palps from the ctenidium to the mouth (Yonge 1959). The gut of *Solemya* is of such extremely reduced size that it alone cannot possibly provide enough nutrient material (Allen and Sanders 1969, p. 388). However, as mentioned above its paradoxically small gut (absent in some species) is probably compensated by its symbiosis with chemoautothrophic bacteria in sulphide-rich levels of the sediment. Possibly *Solemya* uses the lower part of its Y-shaped habit as a connection with its symbionts (suggested by L. Jeppsson).

Autecology of Janeia silurica

The bivalve fauna at Möllbos is dominated by deposit-feeders (90%, Liljedahl 1984) probably reflecting the high silt-clay content of the carbonate sediment (cf. Sanders 1958, 1960). *J. silurica* comprises approximately 20% of all deposit-feeding bivalves and is the third commonest species.

There are facts in favour of niche diversification between the different deposit-feeders at this locality (Liljedahl in press). *J. silurica* is believed to have inhabited a somewhat deeper level in the sediment than the remaining deposit-feeders (Liljedahl 1984, fig. 34). It may have lived symbiotically with chemoautotrophic bacteria at a sulphide-rich level of the bottom (like *S. velum*, see Cavanaugh *et al.* 1981) where it did not have to compete for food with other species (cf. discussion above of extremely reduced size and absence of gut in *Solemya*).

The hypothesis that *J. silurica* was not as specialized a passive suspension-feeding deposit-feeder as the extant *Solemya* but instead was an active burrower, is supported by the assumed differences in the size of the foot and ctenidia of this species and *Solemya*. The absence of a gape in *J. silurica* would have given this species an advantage while burrowing, in preventing excessive sediment from entering the mantle cavity. The almost stationary *Solemya*, on the other hand, has no need of completely closed shell margins. Instead the valves gape at each end, which is advantageous since it can inhale and exhale with the valves closed.

The assumed robust ligament construction of *J. silurica*, in combination with the edentulous hinge and deeply incised, large, subequal adductor muscle scars, may have made it possible for this species to close the valves quickly and vigorously as in *Solemya* (cf. Yonge 1941, p. 115) and with greater force and speed than in nuculoids. These have interlocking hinge teeth which are considered a hindrance to such rapid contraction.

The conspicuous impressions of the pallial muscles, as well as the inferred morphology of the foot and accessory muscles, suggest that *J. silurica* could infold the (fused?) ventral margin of the mantle and simultaneously withdraw the foot, possibly in much the same way as in *Solemya* (see Yonge 1941, p. 136). Thus, *J. silurica* probably had a system for removing indigestible matter from the mantle cavity, perhaps more effective than in extant nuculoids (cf. living nuculoids; Yonge 1941, p. 83).

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